MORPHOLOGY AND RELATIONSHIPS OF TROCHODENDRON AND TETRACENTRON, I. STEM, ROOT, AND LEAF

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With six plates

INTRODUCTION

Owing to their retention of a primitive cambium and a vesselless type of xylem, *Trochodendron* and *Tetracentron* are fully as significant as the Winteraceae, Degeneriaceae, and Himantandraceae in discussions regarding the origin and phylogeny of the angiosperms. Furthermore, as indicated by Dr. Smith in the preceding article in this Journal, the opinions of taxonomists and morphologists concerning the relationships and classification of the two monotypic genera are exceedingly diversified and contradictory. It seemed advisable, accordingly, to utilize the extensive collections assembled by Dr. Smith as a broad basis for morphological as well as taxonomic re-investigations of these unusually significant genera. In presenting the results of our observations, we shall deal largely with morphological features that are incompletely or inadequately covered in the extensive literature.

XYLEM

The most obvious structural characteristics of the wood of *Trochodendron* and *Tetracentron* were first described by Eichler (9) and Harms (12) and have subsequently been re-described by a succession of investigators, e.g. van Tieghem (22), Solereder (20), Kanehira (13), Sahni (17), Mathiesen (14), and McLaughlin (15). That the xylem of both the primary and secondary bodies of stems, roots, leaves, and inflorescences is entirely devoid of vessels or of vestiges of vessels has been clearly demonstrated by Thompson and Bailey (21) and Bailey and Thompson (3). Although the xylem of *Trochodendron* and *Tetracentron* is of a structurally unique type and not to be confused with that of any other known representative of the angiosperms or of the lower vascular plants, the woods of the two genera are so similar as to render difficult and uncertain the task of determining to which genus certain fossil woods from significant geological horizons of India, Greenland, and the northwestern United States actually are related.

As should be anticipated, see Bailey and Faull (1), the woods of *Trochodendron aralioides* Sieb. & Zucc. and *Tetracentron sinense* Oliv. exhibit certain ranges of anatomical variability not only within different parts of the same tree but also in homologous parts of trees grown under different environmental conditions. The most conspicuous and significant differences in the size and form of cambial initials and *pari passu* in the size,

form, and structural details of tracheary elements, rays, and parenchyma occur in passing from young shoots (e.g. of herbarium specimens) to the outer parts of large mature stems. Numerous specimens of the mature wood of *Trochodendron* are available for comparison with herbarium material, but the largest stem of *Tetracentron* that we have succeeded in obtaining has twelve growth layers and a woody cylinder approximately three centimeters in diameter. This specimen affords valuable clues regarding the succession of structural changes — particularly of the rays — that occur during the normal enlargement of a stem. The final form and distribution of the rays in old wood can be accurately reconstructed from the cambium and inner phloem of bark from an old tree collected by E. H. Wilson (no. *659*).

The available evidence indicates that certain anatomical features of the xylem of *Tetracentron* do not fall within the range of structural variability of *Trochodendron*. The most significant of these are the following. As shown by Thompson and Bailey (21), the first formed secondary xylem of stems and roots of *Tetracentron* is characterized by having numerous broad and abnormally short tracheids that subtend the vascular strands of leaves, buds, branches, and rootlets. These tracheids are profusely pitted on both their tangential and radial walls and appear to facilitate the movement of water from a stem into its appendages, or from rootlets into roots. More or less isolated and sporadically distributed radial seriations of these short tracheids extend outward into the subsequently formed secondary xylem. Whether they ever persist in the outer growth layers of old stems and roots unfortunately cannot be determined at present, but it seems likely that they may be found in tissue which subtends the bases of persistent branches. Such tracheids do not occur, however, in either the first-formed or the later-formed secondary xylem of *Trochodendron*.

The wood parenchyma of *Tetracentron* is of a structurally unique type and unlike that of any other vascular plant with which we are familiar. During the maturation of wood parenchyma in normal, uninjured stems of gymnosperms and dicotyledons, derivatives of the fusiform initials of the cambium divide approximately transversely, *Fig. 10*, forming vertically oriented, uniseriate strands of parenchymatous cells. In *Trochodendron*, the wood-parenchyma strands are uniseriate, *Fig. 11*, but the anticlinal partitions are more or less extensively and obliquely oriented. In *Tetracentron*, a large proportion of the derivatives of the long fusiform initials tend to divide first in more or less extensive, longitudinal anticlinal planes, *Fig. 12*, and subsequently the products of these divisions divide transversely or in various diagonal anticlinal planes. The fully matured parenchymatous strands, therefore, are largely biseriate, except in strands or parts of strands where divisions of the *Trochodendron*-type may have occurred. In transverse sections of normally developed, uninjured wood of Winteraceae, as of various gymnosperms — where the radial seriation of successively formed derivatives of the fusiform cambial initials is not disturbed by the enlargement of vessel members or by excessive apical elongation of

non-perforate tracheary elements — the parenchymatous strands appear as single cells of approximately the same tangential diameter as the tracheids. On the contrary, in transverse sections of the wood of *Tetracentron, Fig. 8,* a majority of the parenchymatous strands appear as paired cells and only relatively infrequently as single cells, i.e. where they are sectioned at the level of their tapered ends, *Fig. 12,* or other uniseriate parts. Occasional paired cells are encountered in transverse sections of *Trochodendron* where the uniseriate parenchymatous strands are sectioned at the level of their diagonal partitions, *Fig. 11,* just as three, or even four, such cells may be encountered in transverse sections of *Tetracentron* where the strands are sectioned at appropriate levels, *Fig. 12.*

The wood parenchyma of both *Trochodendron* and *Tetracentron* fluctuates from scanty to abundant, not only in different stems, but also in different growth layers of the same stem. In *Trochodendron,* the parenchymatous strands when abundantly developed tend to be diffusely distributed among the thicker-walled tracheids of the latewood, whereas in *Tetracentron* they may at times be loosely associated in zonal arrangements and may occur in the transitional as well as in the later-formed parts of the growth layers.

The eustele or vascular part of the primary body of stems is composed of more numerous discrete bundles in *Trochodendron* than in *Tetracentron.* This is correlated with significant differences in the number of strands in the leaves of the two genera. Since the first-formed multiseriate rays of the secondary body extend outward from the parenchymatous interfascicular parts of the eustele, the number of such rays in the first-formed growth layer of the secondary body of *Trochodendron* tends to be higher than in the homologous part of *Tetracentron.* During subsequent enlargment of the stems, the relationship becomes reversed,[1] the old wood of *Trochodendron* having conspicuously larger and fewer multiseriate rays per unit area, *Fig. 7,* than does comparable wood of *Tetracentron, Fig. 9.* Furthermore, the rays of the latter genus ultimately attain a more "homogeneous" form, i.e. the cells of the uniseriate rays are less vertically extensive than in *Trochodendron,* compare *Figs. 7* and *9.*

In growth layers of comparable widths and ages, the wood of *Tetracentron* is softer and lighter than that of *Trochodendron,* due largely to the fact that the tracheids of the latewood have thinner walls in relation to their cross-sectional area. In addition, the latewood tracheids of *Tetracentron* are of more uniformly rectangular outline as seen in transverse sections of the wood, and their radial seriation is less disturbed by excessive apical elongation of the tracheary elements during their maturation.

Mathiesen (14) has attempted to differentiate the woods of the two genera by the presence or absence of pits in the tangential walls of the latewood tracheids. Such pits fluctuate, however, from numerous to infrequent in *Trochodendron,* and, in young wood of *Tetracentron,* from very

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[1]For detailed discussions of ray changes that occur during the enlargement of dicotyledons see Barghoorn (4, 5) and Bailey and Howard (2).

abundant (short tracheids) to scanty or absent (normal long tracheids). Not until numerous specimens of the older wood of *Tetracentron* are available for detailed investigation will it be possible to determine whether tracheary pitting provides under all conditions reliable criteria for differentiating the woods of the two genera.

NODAL ANATOMY AND VASCULARIZATION OF THE LEAF

The petioles of the palmately veined leaves of *Tetracentron* have extensive stipular flanges that enclose the much elongated slender buds, *Fig. 35*, except during the final emergent phases of their development. At this level of the petiole, *Fig. 2*, there are three conspicuous vascular strands which tend to broaden and to coalesce at higher levels of the petiole and thus to form a cylindrical stele and a more or less continuous secondary body, *Fig. 1*. The coalescence of the expanded strands and the levels at which specific changes occur fluctuate from petiole to petiole. Not infrequently the vascular cylinder retains an opening or gap in its adaxial side, *Fig. 1*, or this opening may be partly occluded by a detached strand of vascular tissue. At the base of the lamina, the vascular cylinder or cylindrical complex of strands becomes abruptly dissociated into 5–7 bundles which form the principal veins of the leaf. At the nodal level of the stem, three vascular bundles depart from three widely separated parts of the circumference of the eustele, *Fig. 3*, leaving three conspicuous parenchymatous gaps in the secondary body. In other words the nodal anatomy of *Tetracentron* is stereotyped and stable and is characteristically of the so-called trilacunar type.

The highly polymorphic, pinnately veined leaves of *Trochodendron*, *Figs. 23–33*, are exstipulate and only infrequently have buds in their axils. The larger leaves of a pseudoverticil commonly have from 5–7 vascular strands in the base of their petioles, *Fig. 5*. These strands depart from a relatively restricted part of the circumference of the eustele of the stem, *Fig. 6*, and there is much less extensive "girdling" of the lateral bundles than in multilacunar Magnoliaceae. The vascular strands rapidly coalesce, forming an arc, *Fig. 4*, which extends upward through the petiole and midrib of the lamina. This arc-shaped strand may or may not be accompanied in the petiole by two small adaxially detached bundles. The smaller leaves of a pseudoverticil, as also the leaves of juvenile plants, commonly have three vascular bundles, but the strands may at times be reduced to two or even to a single vascular bundle with concomitant modifications in the nodal anatomy of the stem. Thus, the nodal anatomy of *Trochodendron* fluctuates from multilacunar to unilacunar and, in contrast to the stabilized trilacunar condition of *Tetracentron*, is plastic and variable.

SCLERENCHYMA AND SECRETORY IDIOBLASTS

The secondary phloem of *Trochodendron* and *Tetracentron* does not exhibit the precocious flaring of the multiseriate rays and early stratification into narrow alternating arcs of soft bast and fibers that occur so characteristically in Magnoliaceae (*sensu stricto*), Degeneriaceae, and Annon-

aceae. Nor is there a sclerification of the multiseriate rays close to the cambium as in *Euptelea* and many Winteraceae. In bark from old stems of *Trochodendron*, the phloem is characterized by forming large irregular masses of dense non-fibrous, crystal-bearing sclerenchyma. The structurally closely similar sclerenchymatous tissue of *Tetracentron* occurs in less massive, more tangentially oriented clusters, as seen in transverse sections. Nests and diaphrams of sclerenchyma such as are formed so commonly in the pith of various woody ranalian families do not occur in *Trochodendron* and *Tetracentron*.

The leaves of *Trochodendron* are typified by the presence of profusely branching, sclerenchymatous idioblasts which are discussed by Dr. Foster in the following article in this Journal. These bizarre elements project into the large, intercellular spaces of the mesophyll. Similar intercellular spaces and sclerenchymatous idioblasts occur in the cortex of young stems and may be encountered in the pith, particularly in those parts of the stems where the leaves are congested in pseudoverticils. On the contrary, *Tetracentron* is characterized by the occurrence, in the leaf and the outer cortex of both stems and roots, of large more or less extensively elongated or branching secretory idioblasts. These elements have "resinous" contents which stain intensely with sudan IV, but differ markedly in form from the nearly spherical secretory cells of the Winteraceae, Magnoliaceae, and other woody ranalian families.

STOMATA

Solereder (20) described the stomata of *Trochodendron*, *Tetracentron*, *Euptelea*, and *Cercidiphyllum* as being surrounded by several neighboring cells which are not of special form and orientation, in contrast to those of the Magnoliaceae (including *Drimys*, *Illicium*, *Schisandra*, and *Kadsura*) investigated by Vesque (23), where the guard cells are accompanied by subsidiary cells which are oriented parallel to the pore — the so-called rubiaceous type of stomata. On the contrary, Rao (16) maintains that the stomata of *Euptelea* and *Cercidiphyllum* are of Florin's (10) haplocheilic type, whereas those of *Trochodendron* and *Tetracentron* resemble the stomata of other investigated genera of the Magnoliales in being of his syndetocheilic type.[2] It should be emphasized in this connection, however, that Florin's classical investigations of stomata have dealt thus far with gymnosperms and that the terms haplocheilic and syndetocheilic were formulated specifically for use in dealing with gymnosperms. The terms clearly convey implications regarding the morphological form as well as the ontogenetic development of gymnospermous stomata and it is not certain as yet whether they should be adopted in dealing with angiosperms. The available evidence concerning angiospermic stomatal structures, summarized by De Bary (8), Solereder (20), and others, indicates that the morphological form and the ontogenetic development of these structures is exceedingly diversified and variable. Stomata with subsidiary cells oriented

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[2]In the haplocheilic or simple-lipped type the guard cells are formed by a single division of an epidermal initial, whereas in the syndetocheilic or complex-lipped type both guard cells and subsidiary cells are derived from a single epidermal initial.

parallel to the pore may arise as products of the divisions of a single epidermal initial (rubiaceous type) or by divisions of more than one epidermal cell (false rubiaceous type). To classify the stomata of dicotyledonous genera as haplocheilic or syndetocheilic, particularly in discussions of putative relationships between angiosperms and gymnosperms, is at present premature and likely to be misleading.

In all of the numerous gymnosperms figured by Florin (11), with the exception of *Gnetum gnemonoides* Brongn., the guard cells are depressed below the general level of the outer surface of the epidermis and are more or less extensively *overtopped* by adjacent epidermal cells. On the contrary, the guard cells of *Tetracentron* and *Trochodendron* rest in a setting formed by the *subtending* parts of contiguous epidermal cells, *Figs. 13* and *14*. Furthermore, the outer vestibules of the stomata are formed by the cuticular covering of the guard cells rather than by that of neighboring cells, as in those gymnosperms which form such structures. The number, size, and form of the contiguous epidermal cells that are concerned in the formation of the setting for the guard cells fluctuates widely in both genera.

In *Tetracentron,* most of the subtending contiguous cells are of comparatively small size and appear to have been formed by appropriate anticlinal divisions of the larger surrounding epidermal cells, *Figs. 17–19*. Such an inference is strengthened by the not infrequent occurrence of large undivided epidermal cells having extensions which subtend the guard cells, (A) in *Figs. 17–19*. In this genus, the subtending cells usually are not concrescent at the center of the setting, leaving an irregularly shaped opening into the intercellular spaces of the mesophyll, *Figs. 13, 17–19*. At the focal level of the outer surface of the leaf, the narrow, curved, exposed parts of the smaller subtending cells resemble subsidiary cells oriented parallel to the outline of the guard cells. This deceptive similarity to "rubiaceous types" of stomata disappears, however, when adequately prepared material[3] is examined at successive focal levels, *Figs. 17–19*.

[3]Maceration and other techniques developed in connection with the study of cuticles and cuticularized residues of gymnosperms are unreliable in studying various types of angiospermic stomata. We have tested a wide variety of techniques in investigating the stomata of dried dicotyledonous leaves such as may be obtained from herbarium specimens. In dealing with *Tetracentron* and *Trochodendron* two types of preparations are essential. (1) Transverse sections of leaves prepared by soaking pieces of leaves in hot water, dehydrating, embedding in paraffin, serial sectioning, staining in Haidenhain's haematoxylin and sudan IV, and finally mounting the sections in glycerine. (2) Isolated sheets of the epidermis with more or less attached mesophyll for examining the stomata in surface view. Such sheets may be obtained in various ways, one of the most successful of which is the following. Small pieces of re-expanded leaves are attached by their lower surfaces to cover glasses, using Haupt's fixative hardened by formalin vapor. In the case of *Tetracentron,* most of the foliar tissue can then be peeled away, leaving the epidermis attached to the cover glass. In the case of *Trochodendron,* the overlying foliar tissues must be cut away under a dissecting microscope. The adhering epidermal strips are then stained with Delafield's haematoxylin and mounted in clarite. Microtome sections cut parallel to the lower surface of the leaf, obtained and treated as in (1), are also of value in interpreting surface views of the stomata.

The stomata of *Trochodendron* are of a fundamentally similar type, but differ in their more conspicuously developed cuticular vestibules, *Figs. 14–16*, their more extensively submerged contiguous cells, *Figs. 20–22*, and their much higher proportion of centrally concrescent subtending cells. *Figs. 15* and *16*. As indicated in *Figs. 20–22*, many of the subtending cells which form the setting for the guard cells become completely submerged by displacements during the ontogenetic development of the stomata. Thus, at the focal level of the outer surface of the leaf, the guard cells appear to be surrounded, at least in part, by ordinary epidermal cells "which are not of special form and orientation." Only where parts of the subtending cells are externally exposed does one encounter the appearance of narrow subsidiary cells oriented parallel to the outline of the guard cells, right side of *Fig. 21*, left side of *Fig. 22*. In *Figs. 14, 21*, and *22*, there is a narrow slit-like opening in the setting of the guard cells which communicates with the intercellular spaces of the mesophyll. In *Figs. 15* and *20*, the subtending cells are concrescent at the center of the setting and the passageway is closed. In *Fig. 16*, there is a broad cuticularized layer between the guard cells and their subtending, contiguous epidermal cells.

It seems likely that from a solely ontogenetic viewpoint of cell lineages, the stomata of *Tetracentron* and *Trochodendron* may be likened to Florin's haplocheilic gymnospermous type, but actually they are of a fundamentally different morphological form. Not until the stomata of a wide range of the Ranales and other orders have been carefully re-investigated will it be possible to assess the phylogenetic significance of different stomatal structures in discussions regarding the origin and the relationships of the dicotyledons.

It should be emphasized, in these connections, that the stomata and the vascular tissues of *Tetracentron, Trochodendron*, and the Winteraceae are of unusual interest from physiological as well as morphological points of view. They provide three distinctly different anatomical-physiological systems in vesselless plants with broad leaves that deserve intensive experimental investigation. The more or less conspicuously coriaceous leaves of the Winteraceae have stomata that are "plugged" by an alveolar modification of the cuticle. In these plants, there is an evident tendency to eliminate scalariform tracheary pitting. On the contrary, *Tetracentron* and *Trochodendron* have scalariformly pitted tracheids in the earlier-formed part of their growth layers. The coriaceous leaves of *Trochodendron* exhibit stomatal and other adaptations for retarding transpiration. The leaves of *Tetracentron* do not have such obvious morphological modifications for reducing water-loss, but there are conspicuous tracheary adaptations which appear to facilitate a more rapid flow of water from stems into leaves and from rootlets into roots.

PALAEOBOTANICAL CONSIDERATIONS

Among the abundant, palmately veined, dicotyledonous leaves of Cretaceous and early Tertiary strata are many which were referred by the earlier palaeobotanists to such heterogeneous form genera as *Populus,*

Populophyllum, Celastrophyllum, etc.   More recently Berry (7), and sub-sequently Seward and Conway (19), Sanborn (18), and others have recognized that the form and the venation of certain of these leaves so closely simulate those of *Cercidiphyllum* and *Tetracentron* as to indicate that they probably belong either to these genera or to closely related plants.   The hypothesis that *Trochodendron* and *Tetracentron* or their allies were widely distributed in Holarctica during pre-glacial times is strongly supported by the occurrence of characteristic vesselless fossil wood in India, the north-western United States, and East Greenland and of a fruit and seeds of *Trochodendron*-like type in the London Clays.

The re-examination of fossilized dicotyledonous floras to insure more accurate and reliable identifications of individual components of such floras is clearly a task for palaeobotanists, but the palaeobotanist must rely upon taxonomists and morphologists for basic data regarding extant dicotyledons and for clues concerning critical diagnostic criteria that may be preserved in fossilized material.   It is advisable, accordingly, to summarize certain of our morphological observations for possible future palaeobotanical use, particularly as they are based upon the most extensive collections of *Trochodendron* and *Tetracentron* that have ever been assembled for in-vestigation.

The leaves of *Trochodendron aralioides* Sieb. & Zucc., the only surviving species of the genus, are highly polymorphic, as illustrated in *Figs. 23–33*. Although certain of the diverse foliar forms may ultimately be shown to be correlated with specific geographical races or genetically significant vari-eties, the available evidence indicates that many, if not most of them, are due to ontogenetic and environmental influences and may occur on a single tree, either simultaneously or during successive stages of its growth to maturity.   In any case, the polymorphism is so extensive that it should be reckoned with in any search for *Trochodendron* in fossil floras, as in the revision of heterogeneous form genera.

To insure a higher degree of diagnostic reliability, the student of dicoty-ledonous fossils must ultimately resort in many cases to techniques com-parable to those which are being used so profitably in studying the foliar organic residues of gymnosperms and ferns.   The chemically and mechan-ically most resistent, and therefore the structurally most persistent, parts of leaves commonly are the cuticularized and heavily lignified parts, i.e. the cuticle and epidermis, sclerenchyma, and xylem.   The foliar cuticle of *Trochodendron* is very thick and forms distinctive stomatal vestibules, the sclerenchymatous elements are characteristically bizarre, and the vesselless xylem occurs in specific structural patterns within the petiole.

The palmately veined leaves of *Tetracentron sinense* Oliv. exhibit a much less extensive variability in external form than do the pinnately veined ones of *Trochodendron*.   As indicated in *Figs. 34–39*, the leaves fluctuate some-what in size, in breadth as related to length, in the degree of fineness of their serrations, in the contour of their bases and in their symmetry, but their range of variability does not overlap that of the conspicuously dimor-

phic foliage of *Cercidiphyllum japonicum* Sieb. & Zucc., which we shall discuss in a subsequent paper. Difficulties in differentiating the leaves of *Tetracentron* and *Cercidiphyllum* in fossil floras may be anticipated only upon the assumption that the ranges of morphological variability in hypothetical extinct species of the two genera tended to overlap. To clarify such putative uncertainties by resorting to microscopic analyses of foliar organic residues is likely to prove more difficult than in the case of the tough coriaceous foliage of *Trochodendron*. The leaves of *Tetracentron* and *Cercidiphyllum* are soft and delicate, having tenuous cuticles and no strikingly distinctive sclerenchymatous features. The highly characteristic secretory cells of the lamina of *Tetracentron* are unlikely to be preserved in recognizable form. A more profitable preliminary line of palaeobotanical endeavor in dealing with *Tetracentron* would appear to be a search for leaves with intact petioles or associated fragments of vesselless stems. As indicated earlier, the petioles of this genus are characterized by having extensive, bud-enclosing, stipular flanges, whereas the petioles of *Cercidiphyllum* are not. It is of interest in this connection that, according to Berry (7), many of the earliest known dicotyledonous leaves of late Lower Cretaceous horizons had petioles which enclosed the buds.

There is obviously no difficulty in differentiating the pinnately veined leaves of *Trochodendron* from the palmately veined ones of *Tetracentron*. Existing palaeobotanical uncertainties are due to superficial similarities in form and venation of the leaves of these genera and of other remotely related dicotyledons. On the contrary, the vesselless woods of *Trochodendron* and *Tetracentron* are remarkably similar, but are unlike the xylem of any other known representatives of the angiosperms. Thus, although the fossilized vesselless woods described by Sahni (17), Mathiesen (14), and Beck (6) should be compared to *Trochodendron* and *Tetracentron*, there is at present considerable uncertainty as to which genus they are more closely related. The most significant of these fossils is Sahni's *Homoxylon rajmahalense*, from the Rajmahal Hills of India, since it may prove to be of Jurassic age and would thus become the earliest known representative of the angiosperms. The specimen is a fragment of wood from a stem of relatively large size. There is no attached bark and the pith and earlier growth layers are not included. Sahni's description of the specimen is based largely upon comparison with *Trochodendron*, no wood of *Tetracentron* having been available for comparative purposes. The size, form, and description of the rays in *Homoxylon rajmahalense* are, however, of the type illustrated in *Fig. 9,* and are indicative of closer relationship to *Tetracentron* than to *Trochodendron*. It is essential that the specimen be reexamined to determine whether the wood parenchyma is likewise of the type which occurs in the former genus.

Beck's (6) specimen of vesselless wood from a Tertiary horizon of the northeastern United States resembles *Homoxylon rajmahalense* in its grosser features and in having rays that are suggestive of *Tetracentron* rather than of *Trochodendron*. The wood parenchyma of this specimen

also deserves detailed re-investigation. In the case of Mathiesen's (14) *Tetracentronites Hartzi*, from an Eocene horizon of East Greenland, both the rays and the wood parenchyma need to be re-examined for evidence of affinities to *Tetracentron* or *Trochodendron*.

It is unfortunate that none of these specimens of vesselless dicotyledonous wood include the pith, since the primary body, nodes, and first-formed secondary xylem of stems afford distinctive and reliable criteria for differentiating *Tetracentron* from *Trochodendron*. In dealing with fossilized dicotyledonous wood, it is essential for collectors to search for and to preserve both the earlier and the later-formed parts of stems. Similarly, in collecting such botanically significant leaves as those of *Trochodendroides*, a careful search should be made for fragments of small shoots which may occur within the same matrix. For, if they prove to be vesselless, they provide strong corroborative evidence for excluding *Populus*, *Cercidiphyllum*, *Grewia*, and other vessel-bearing genera whose leaves have at times been confused with those of *Tetracentron* or of *Trochodendron*.

It should be emphasized, in conclusion, that available palaeobotanical evidence, although fragmentary and uncertain in specific instances, indicates as a whole that *Tetracentron* and *Trochodendron* or closely allied plants have a very extensive geological record, extending backward to the late Lower Cretaceous, and possibly to the Jurassic in the Rajmahal horizon of India. These plants appear to have been widely distributed through Holarctica during pre-glacial times and only subsequently to have been confined to "relic" Asiatic areas.

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EXPLANATION OF PLATES

PLATE I

FIG. 1. *Tetracentron, H.U. 18052.* Transverse section of upper part of petiole, × 21. FIG. 2. *Tetracentron, H.U. 18050.* Transverse section of lower part of petiole, showing enclosed bud, × 25. FIG. 3. *Tetracentron, H.U. 18053.* Transverse section of stem at level of trilacunar node, × 25. FIG. 4. *Trochodendron, H.U. 18093.* Transverse section of upper part of petiole, × 27. FIG. 5. *Trochodendron, H.U. 18082.* Transverse section of basal part of petiole, × 21. FIG. 6. *Trochodendron, H.U. 18072.* Transverse section of stem at level of multilacunar node, × 11.

PLATE II

FIG. 7. *Trochodendron, H.U. 8383.* Tangential longitudinal section of wood from a large stem, showing form and distribution of the rays, × 50. FIG. 8. *Tetracentron, H.U. 9695.* Transverse section of the wood, showing paired parenchymatous cells; the radially seriated derivatives of the cambium are oriented crosswise of the page, × 500. FIG. 9. *Tetracentron, Wilson 659.* Tangential longitudinal section of the cambium and inner phloem of bark from an old tree, showing form and distribution of rays, × 50.

PLATE III

FIG. 10. Typical transverse planes of anticlinal division in the formation of the uniseriate wood-parenchyma strands of most gymnosperms and dicotyledons. FIG. 11. *Trochodendron.* Diagonal anticlinal divisions in the formation of the uniseriate wood-parenchyma strands. FIG. 12. *Tetracentron.* Longitudinal and diagonal planes of anticlinal division in the formation of biseriate wood-parenchyma strands. FIG. 13. *Tetracentron, Wilson 659.* Transverse section of a stoma, showing cuticular vestibule, guard cells, and subtending contiguous epidermal cells, approx. × 270. FIGS. 14-16. *Trochodendron. Jack,* in 1905. Transverse sections of stomata showing cuticular vestibule and three types of settings for the guard cells, approx. × 270.

PLATE IV

Borders of the cuticular vestibule densely stippled. Guard cells less densely stippled. Exposed parts of contiguous epidermal cells lightly stippled. Submerged parts of contiguous cells indicated by broken lines.

FIG. 17. *Tetracentron, Wilson 659.* Surface view of stoma, showing guard cells with their partly subtending contiguous epidermal cells; (A) large subtending cells, approx. × 675. FIGS. 18, 19. *The same.* Less highly magnified surface views of stomata, showing various patterns of contiguous epidermals cells; (A) large subtending cells, approx. × 320. FIGS. 20-22. *Trochodendron, Jack,* in 1905. Surface views of stomata, showing varying degrees of submergence of the contiguous epidermal cells, approx. × 675.

PLATE V

Leaves of *Trochodendron aralioides* Sieb. & Zucc., one-half natural size.

FIG. 23. *Takenouchi 1017.* FIG. 24. *Faurie 3643.* FIG. 25. *Wilson 9716.* FIG. 26. *Simada 876.* FIG. 27. *Sasaki 351.* FIG. 28. *Wilson 11231.* FIG. 29. *Mayr,* in 1886. FIG. 30. *Takenouchi 1017.* FIG. 31. *Gressitt 197.* FIG. 32. *Wilson 9716.* FIG. 33. *Jack,* in 1905.

PLATE VI

Leaves of *Tetracentron sinense* Oliv., one-half natural size.

FIG. 34. *Henry 6243.* FIG. 35. *Tsai 57831.* FIG. 36. *Wilson 659a.* FIG. 37. *Cheng 3419.* FIG. 38. *Cheng 3419.* FIG. 39. *Wang 67836.*

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